Journal of
Marine Science and Engineering

MDPI

Article

Modeling the Habitat Distribution of *Acanthopagrus schlegelii* in the Coastal Waters of the Eastern Taiwan Strait Using MAXENT with Fishery and Remote Sensing Data

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Citation: Teng, S.-Y.; Su, N.-J.; Lee, M.-A.; Lan, K.-W.; Chang, Y.; Weng, J.-S.; Wang, Y.-C.; Sihombing, R.I.; Vayghan, A.H. Modeling the Habitat Distribution of *Acanthopagrus schlegelii* in the Coastal Waters of the Eastern Taiwan Strait Using MAXENT with Fishery and Remote Sensing Data. *J. Mar. Sci. Eng.* **2021**, *9*, 1442. https://doi.org/10.3390/jmse9121442

Academic Editor: Dariusz Kucharczyk

Received: 19 October 2021
Accepted: 14 December 2021
Published: 16 December 2021

Abstract: Black sea bream, *Acanthopagrus schlegelii*, is among the most commercially valuable species in the coastal fishery industry and marine ecosystems. Catch data comprising capture locations for the gillnet fisheries, remotely sensed environmental data (i.e., sea surface temperature, chlorophyll-a concentration, and current velocity), and topography (bathymetry) from 2015 to 2018 were used to construct a spatial habitat distribution of black sea bream. This species is concentrated in coastal waters (<3 nm) from December to April (spawning season). The maximum entropy (MaxEnt) method and corresponding habitat suitability index among seasons were used to clarify the species' spatial distribution and identify the seasonal variations in habitat selection. The patterns corresponded closely to the changes in oceanographic conditions, and the species exhibited synchronous trends with the marine environment's seasonal dynamics. Chlorophyll-a concentration and bathymetry substantially influenced (80.1–92.9%) black sea bream's habitat selection. By applying the MaxEnt model, the optimal habitats were identified with four variables including depth and satellite-derived temperature, current velocity and chlorophyll-a concentration, which provides a foundation for the scientific assessment and management of black sea bream in coastal waters of the Eastern Taiwan Strait.

Keywords: habitat selection; environmental variation; habitat suitability index; maximum entropy

1. Introduction

Fish are a main source of food, and they account for 16.6% of the global consumption of animal protein and 6.5% of all protein consumption [1]. The global catch serves more than 2.6 billion people and provides at least 20% of their average annual protein intake [2]. Changes in marine environments affect both species composition and spatial distribution. Changes thereof can further influence catch potential over the years, and reflect troubling patterns of global climate change in the world's oceans and the changes in fishery resources. Concerns over the impact of climate change on marine ecosystems are growing, and long-term changes in mean environmental conditions and climatic variability have exceeded the limits of what marine communities can adapt to [3–5].

Taiwan has experienced a decrease in catch potential in recent decades. Studies have reported decreases in catch in the waters off central Taiwan and Penghu [6]. This trend has been caused by pollution, damage to marine environments, invasive species, and climate change. Overfishing and the overuse of fishery resources are threatening marine species [6,7]. Studies have also indicated that from 2005 to 2055, the catch potential of the tropical Pacific Ocean could decrease by 42% [8]. The repercussions of climate change are expected to affect tropical and high-latitude regions of the Pacific Ocean. Consequently, these changes will substantially affect global fishery production and, therefore, the food supply sourced from marine life [8–10]. Given the increased exposure of marine ecosystems to various natural and anthropogenic effects, identifying and characterizing marine hotspots in habitat spatial distribution is essential when establishing conservation priorities and evaluating management strategies [11,12].

Black sea bream, *Acanthopagrus schlegelii*, is among the most commercially valuable species captured in coastal fisheries off Taiwan. This species is widely distributed in the coastal waters of tropical and temperate regions of the Pacific Ocean [13] and is widely consumed in Japan, Korea, Taiwan, China, and Vietnam because of its excellent meat quality (which gives it considerable market value). Black sea bream can tolerate a wide range of environmental conditions, and they exhibit high resistance to disease [14,15].

Numerous studies have been conducted over the years on the biology, ethology, and population of black sea bream in the coastal waters of the western Pacific Ocean [16–19]. Black sea bream spawning seasons are supported by high rainfall, temperature, and relative humidity. Analyses of their reproductive biology have indicated that male black sea bream can switch their sex to female (protandric hermaphrodite). Their habitats are influenced to a certain extent by the season, selection, water temperature, chlorophyll concentration, depth, and velocity construct in a habitat environment [20,21]. However, these studies provided limited insights into the behavior of the species and its response to environmental changes and oceanographic variations [22]. Improvements in scientific research have led to the emergence of novel analytic techniques that have been developed to clarify the interactions between species and their habitat selection. Species and environment interaction studies are necessary because they allow for the development of predictive models based on the hypothesis that a fish species selects the optimal habitat on the basis of both biological and environmental factors [23,24], and such models can be used as foundations for fishery management.

In a marine ecosystem, hydrological variables are frequently used as proxy indicators to examine the effects of biological–physical processes on species abundance and distribution [25,26]. Maximum entropy (MaxEnt) modeling is a method for predicting the geographical distribution of a species and environmental variables through the use of occurrence data; users are allowed to fit a model of arbitrary complications [27]. Satellite-derived data are now available and commonly used with a maximum entropy algorithm to construct species distribution models [28,29]. These models can map the spatiotemporal distribution of a species in multiple areas in response to key environmental parameters, with potential use in fishery management [30,31].

The yield from coastal and offshore capture fisheries in Taiwan has decreased substantially since 1980, and a reduction of more than 50% has been reported in recent years [32]. Black sea bream production from capture fisheries has decreased substantially, and this trend is apparent in waters off northern and central Taiwan. It could be caused by environmental changes such as a higher sea surface temperature, which influences the growth, feeding, reproduction, and habitat of fish in the ocean and, consequently, reduces their populations. A higher sea surface temperature also affects seasonal catches, such as those of mullet. This seasonal migration indirectly affects the catch composition and abundance of fishery resources [6,33,34].

Black sea bream is now recognized as an overfished species in Japan and Taiwan. It is categorized as threatened due to eutrophication, pollution such as solid waste, and climate change, which causes habitat loss and degradation [35,36]. Local management agencies are concerned about the aforementioned problems. Fisheries are highly complex and diverse in the coastal and offshore waters of western Taiwan [33,37]. Teng et al. [38] reported that the main fishing ground of coastal and offshore fisheries off western Taiwan is located in the waters of Chang-Yun Rise. The study also indicated that the hydrological condition of the coastal waters off south-western Taiwan is more stable and warmer relative to other sites [39]. The hydrological condition and biological features influence species composition, and they comprise current speed, current direction, oxygen, chlorophyll-a concentration, and zooplankton [33]. Northwestern Taiwan is often affected by monsoons, and this factor increases the difficulty of fishing for local fisherman [39]. Monsoons can benefit fish by providing an abundance of nutrients in summer through upwelling; specifically, the China Coastal Current (CCC) that occurs in the Taiwan Strait (TS) produces the highest nutrient concentration around the coast in winter. These phenomena may contribute to the abundance of fishery resources [40,41].

Understanding black sea breams' changing habitats by modeling their habitat distribution is essential. As wild fish, they are difficult detect in their natural habitat in the ocean. Accordingly, the present study aimed to summarize a narrow set of environmental variables by examining a large pool of biologically critical data sets of factors that may influence the habitats of black sea bream seasonally in the coastal waters off Taiwan; the data sets were then used in habitat models to examine seasonal variations in spatial distribution. We further investigated the stability and persistence of habitats by using high-resolution data and a simple method that involved spatial predictions of black sea bream habitats, and we also identified potential habitat hotspots in coastal waters.

2. Materials and Methods

2.1. Study Area

Fishery data were collected from randomly selected coastal and offshore gillnet vessels operating in waters off western Taiwan within the range of 21.5° N to 25.5° N and 119.5° E to 122.5° E (Figure 1). The TS connects the East China Sea (ECS) with the South China Sea (SCS) in the area between Taiwan and China in the western Pacific Ocean [42]. The Chang-Yun Rise is a distinct topographical feature of the TS that extends westward from the coast of western Taiwan. Instead, the current pattern changes frequently in winter in the TS; specifically, the CCC usually travels through the western TS and moves southward along the coast of eastern China. The branches of the Kuroshio Current (KBC) and South China Sea Warm Current (SCSWC) meet in the TS and exchange water and nutrients [43].

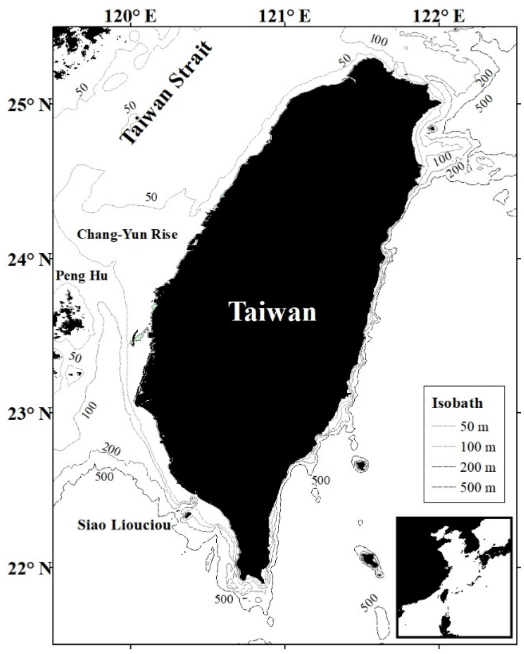


Figure 1. Map of study area (21.5° N–25.5° N and 119.5° E–122.5° E) and topographic features (isobaths as shown in dotted line).

2.2. Fishery Data

Catch and effort data based on daily logbooks for the coastal gillnet vessels were collected between 2015 and 2018. Daily information on fishing locations (longitude and latitude represented at a 0.01° × 0.01° grid resolution), catch in numbers and weight by species, and fishing date was included in the dataset, which was subsequently used in the habitat model analyses for black sea bream. Black sea bream is a target species of coastal gillnet fisheries; thus, the catch per unit effort (CPUE) data collected from the gillnet fisheries can serve as an indicator of fishery resources and their habitat spatial distributions [44].

The CPUE of fishing grid i (0.01° × 0.01°) by season was calculated using the following equation:

$$CPUE_{s,i} = \frac{\sum C_{s,i}}{\sum E_{s,i}} \quad (1)$$

where $\sum C_{s,i}$ is the total catch in weight (kg) of fish caught from sampled fishing vessels within grid i of the fishing location in season s, and $\sum E_{s,i}$ is the size of the gillnet used in fishing grid i during season s; for each operation, the fishermen reported the total length and width of the net used. In consideration of varying fishing operations and characteristics and hydrological conditions, we divided the coastal fishing ground off western Taiwan into three sections, namely north (24.4° N–25.5° N), central (23.5° N–24.4° N), and south (21.5° N–23.5° N).

2.3. Environmental Parameters

Two types of environmental data were used for the analysis, namely remote sensing and geological data (Table 1). The remote sensing data included satellite-derived sea surface temperature (SST) data, which were measured with advanced high-resolution radiometer (AVHRR) sensors and collected from the regional AVHRR data library at National Taiwan Ocean University [45]. SST images were produced using a multichannel SST algorithm at a spatial resolution of 1.1 km [46]. The chlorophyll-a (Chl-a) concentration data were obtained using moderate-resolution imaging spectroradiometer sensors from the National Aeronautics and Space Administration [47]. The Chl-a images featured the same spatial resolution (in 1.1 km) as the SST images.

Table 1. Environmental parameters used to construct habitat model for black sea bream in coastal waters of Taiwan.

Environmental Variables	Sampling Interval	Spatial Resolution	Primary Source
Sea surface temperature (°C)	Daily	0.01°	AVHRR
Chlorophyll-a concentration (mg/m^3)	Daily	0.01°	MODIS
Current velocity (m/s)	Daily	1/12°	HYCOM
Bathymetry (m)	-	1/60°	ETOPO1

For the HYbrid Coordinate Ocean Model (HYCOM), a primitive equation was used to determine a general circulation model [48]. A HYCOM with a 1/12° horizontal resolution at the equator (approximately 7 km at mid-latitudes) is the ocean model component of an eddy-resolving operational forecasting system. In the present study, HYCOM data were used to simulate differences in current circulation at the surface of the study area. We further compared the SST images from AVHRR and HYCOM to evaluate potential differences from multiple sources. For the topographic data, 1/60° bathymetric data were collected from the ETOPO1 Global Relief Model released by the National Oceanic and Atmospheric Administration.

2.4. Development and Evaluation of Habitat Model

CPUE is generally regarded as a reliable proxy for species presence and abundance, and it is increasingly used to develop habitat models [49–52]. Therefore, CPUE data from sampling fishing vessels were used in the present study to develop a spatial distribution model with a narrow set of environmental data that were subsequently used to identify potential black sea bream habitats. The distribution model of the species was based on the MaxEnt algorithm and a generative method. The MaxEnt model (software version 3.4.1) is commonly used in habitat studies for both terrestrial [53] and marine applications [54]. In the present study, 10% of high CPUE data were used in the test model, and 10 iterations of bootstrapping were performed to sample high CPUE data to develop the habitat model [25,31,54].

The MaxEnt model is a freely available software used to identify and map the key habitats of various marine species [25,31,55]; thus, it was selected to determine the potential habitats of *A. schlegelii* and to examine the seasonal variation of their habitat distributions. The framework is based on the maximum entropy principle, which predicts the probability of species distribution subject to constraints from available data on environmental conditions and species occurrence. The MaxEnt model can identify changes in the influence of environmental variables on the distributions across seasons that are likely associated with their life history. The habitat suitability index (HSI), based on the predictions from the MaxEnt models, was used to evaluate the potential habitat; the HSI values range from 0 to 1, with the values closer to 1 representing a habitat condition preferred more by black sea bream, with values near 0 indicating unsuitable habitat conditions. The MaxEnt models were developed to evaluate the inclusion of environmental and geographical factors that can affect black sea bream habitats.

We used spatially matched black sea bream fishing data (response variables) and environmental parameters (independent variables) to develop our habitat models based on MaxEnt. The criterion of area under the curve (AUC) was used, and the percentage contribution of each variable was selected according to the constructed final MaxEnt model [56]. The response curves generated from each model were examined to deduce the environmental range of the potential black sea bream habitats that were identified in the study area. The intersections of the response curve and preferred suitable indices were used to determine the optimal range of the environmental variables [25,31,54].

2.5. Spatial Mapping and Validation

The fishery data and corresponding environmental variables were then applied to the selected model to validate the habitat model. The environmental data for each season were used as inputs for the model to predict the spatial distribution of the fish habitat. The seasonal spatial patterns of the black sea bream habitats were evaluated based on the spatial predictions averaged over multiple seasons. Pixel-wise standard deviations (SDs) over the seasons of the study period were calculated to provide a measure of the uncertainty for spatial habitat prediction [31,57]. Finally, the spatial distribution predicted using the MaxEnt model and SDs was mapped over seasons (using ArcMap version 10.1 software, ESRI Inc.; Redlands, CA, USA), and compared with observed fishery data from the sampled gillnet fishing vessels to evaluate the performance of the model predictions, with respect to the potential fishing grounds of this species.

3. Results

3.1. Seasonal and Environmental Effects

The monthly production of the sampling vessels in this study was presented from 2015 to 2018, which indicates a strong seasonal fluctuation (Figure 2). The primary fishing period for the black sea bream fishery lasts from December to April. The south section achieved a higher production of black sea bream during most months; however, the north and central sections achieved higher production levels in spring and early summer. Figure 3 presents the spatial distributions of black sea bream derived from the data collected from the gillnet fisheries in the coastal waters off Taiwan. In spring, high black sea bream CPUE was concentrated in coastal areas; specifically, high CPUE (red grid) was observed in Chang-Yun Rise (approximately 24.1° N). In summer, the high CPUE area shifted with the latitudinal distribution centroid moving northward (25.3° N) and southward (23.5° N). The high CPUE area was primarily concentrated in coastal waters off southwest Taiwan in autumn and winter, and a subsequent peak in distribution was observed in Chang-Yun Rise in winter.

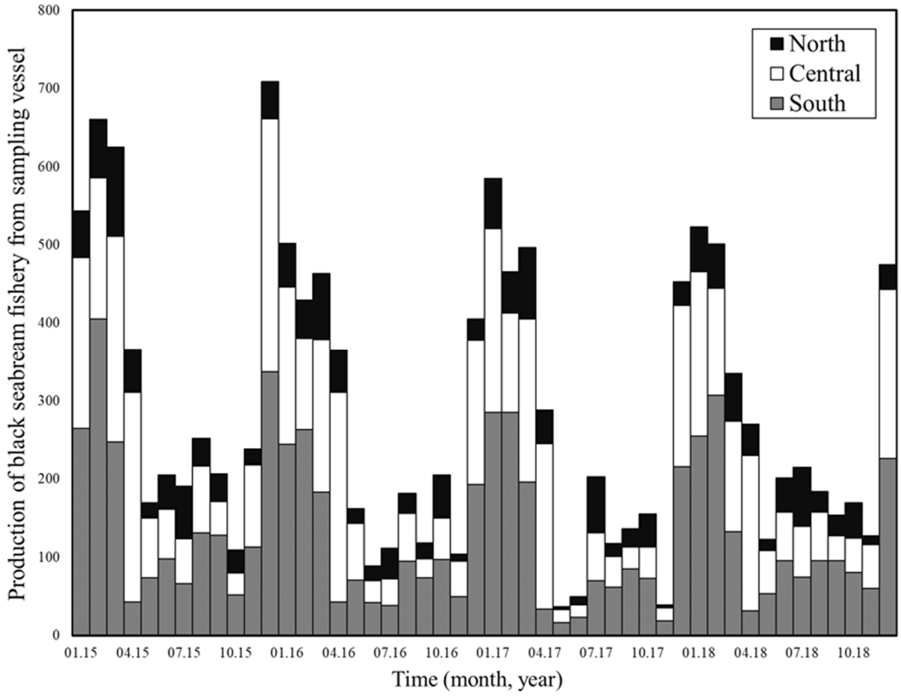
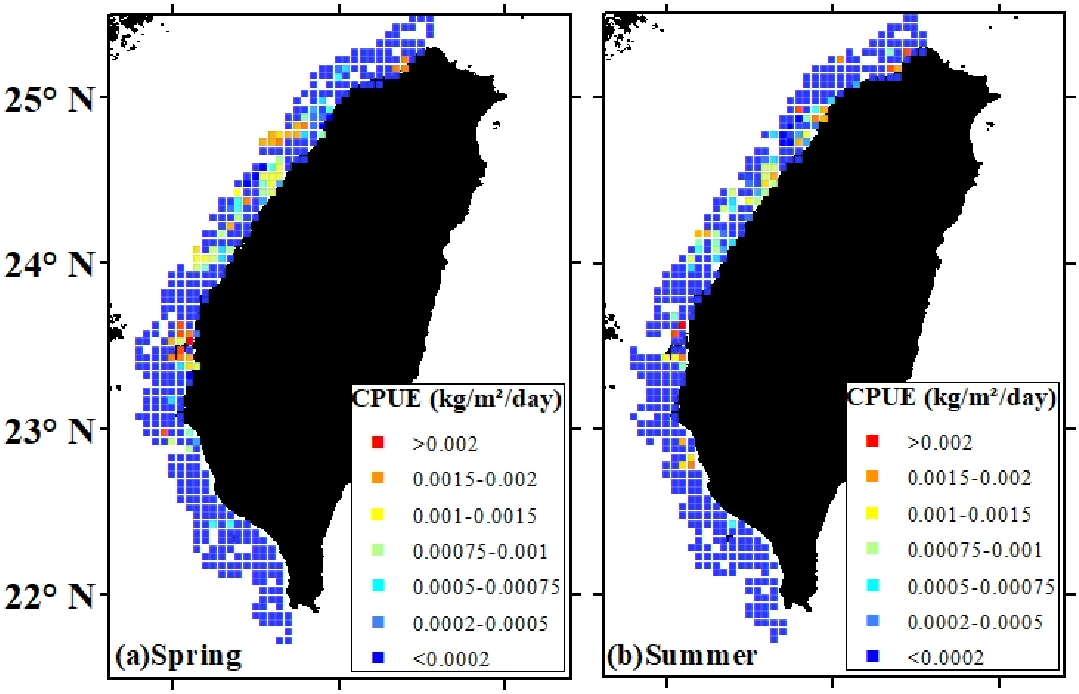


Figure 2. Monthly production of black sea bream from coastal and offshore fisheries in waters off western Taiwan from 2015 to 2018.



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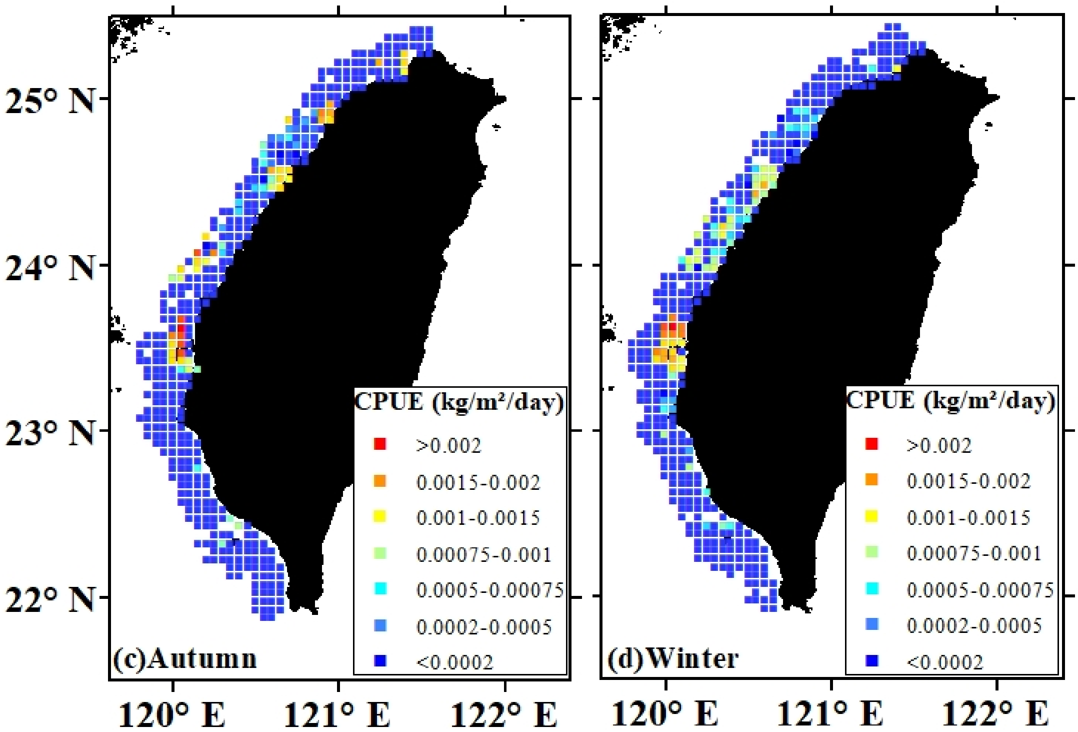
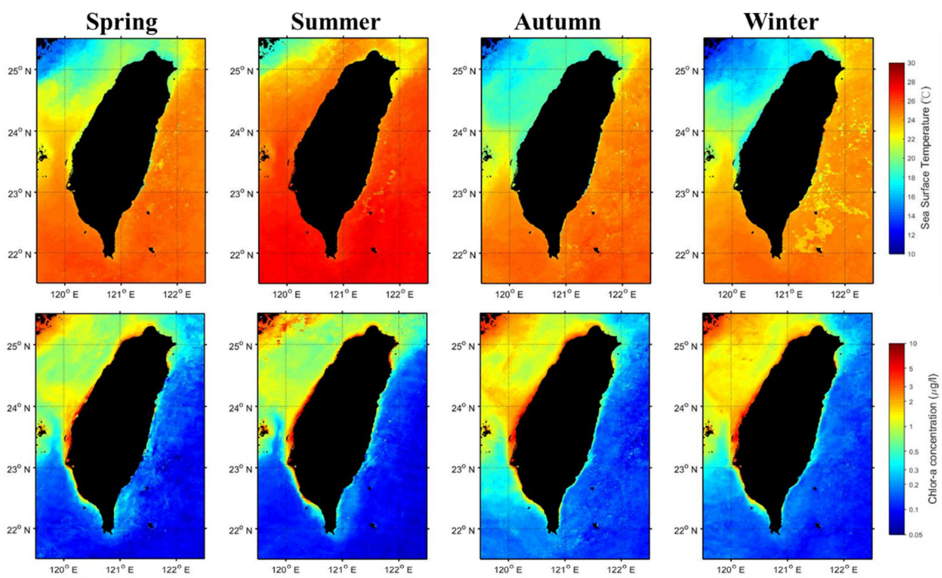


Figure 3. Catch per unit effort, CPUE (kg/m^2) distributions of black sea bream from sampled gillnet vessels by season in waters off western Taiwan.

Seasonal variations in the environmental variables were observed over the study period (Figure 4). The spatial maps of the environmental variables used in the MaxEnt models indicated that monthly SSTs and their spatial patterns prevailed when the northeast winter monsoon entered the TS; hence, SST in the TS remained at 19 °C throughout the winter. However, the southwest spring and summer monsoon caused a branch of the Kuroshio Current to enter the TS, resulting in a higher SST of between 26 and 28 °C in the area. The spatial patterns of Chl-a concentration exhibited no significant seasonal variation. The CCC contained high levels of Chl-a; therefore, the TS exhibited high concentrations of Chl-a in autumn and winter, but the velocity of flow in the waters off southwestern Taiwan was lower than in other areas because of the geographical shield provided by the Penghu and Siaoliouciou Islands.



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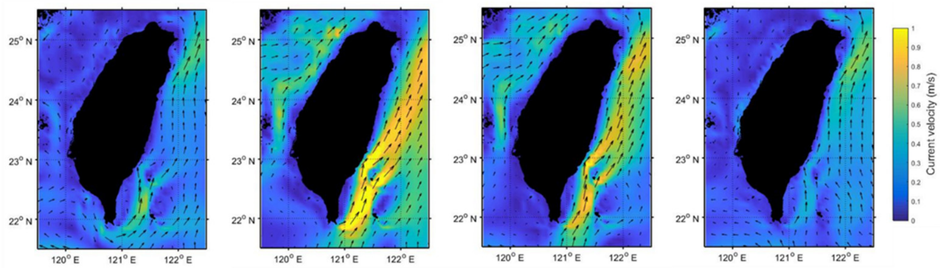

Figure 4. Spatial distributions of environmental variables (used in MaxEnt habitat model) by season within study area from 2015 to 2018.

3.2. Environmental Conditions in Black Sea Bream Habitats

The relative and variable contributions of multiple oceanographic and topographic factors (Table 2) were used to develop seasonal MaxEnt habitat models. The Chl-a and bathymetry were revealed to be highly influential on and significant (80.1–92.9%) to black sea bream habitats across all four seasons. Compared with the other environmental variables, the current velocity exhibited low to almost negligible significance on the predictions of black sea bream habitat for all four seasons (<3%). Table 2 indicates that the average training AUC of each season was higher than 0.9 and provides the average test AUC of each season. These results indicated a good performance in modeling and the absence of over-fitting in the model.

Table 2. Relative contribution of environmental variables used to construct habitat model by season.

Environmental		Percent	Contribution	
Variables	**Spring**	**Summer**	**Autumn**	**Winter**
Chl-a	59.1	64.6	71.3	80.3
Bathymetry	21	22.7	20.1	12.6
Current Velocity	0.3	1.6	1	2.2
SST	19.6	11.1	7.6	5.9
Test AUC	0.949	0.955	0.959	0.967
Training AUC	0.973	0.978	0.966	0.979

In summer, SST, Chl-a, bathymetry, and current velocity exhibited ranges of 24.5–31 °C, 0.01–8.03 mg m^{-3}, 0–300 m, and 0.02–1.17 m s^{-1}, respectively. However, in autumn, SST, Chl-a, bathymetry, and current velocity exhibited ranges of 24–28.2 °C, 0.06–8.13 mg m^{-3}, 0–300 m, and 0.01–0.85 m s^{-1}, respectively. In winter, the black sea breams' preferred habitat was influenced by SST, Chl-a, bathymetry, and current velocity, which ranged between 12.7 and 26.6 °C, 0.1 and 8.2 mg m^{-3}, 0 and 300 m, and 0 and 0.71 m s^{-1}, respectively. In spring, high HSI values (>0.7) were observed at the ranges of 20.6–28.9 °C for SST, 0–15 m for bathymetry, and 0.28–0.83 m s^{-1} for current velocity. Thus, elevated Chl-a was determined to have a positive effect on black sea bream habitats when Chl-a was lower than 4.6 mg m^{-3} throughout the year.

Figure 5 presents the response curves of the environmental effects derived from the seasonal MaxEnt models. The optimal ranges (HSI > 0.7) for bathymetry were similar (0–15 m) for each season. The potential habitat of the black sea bream was influenced by SST, Chl-a, bathymetry, and current velocity in spring, with these variables exhibiting ranges of 15.8–27.9 °C, 0–8.13 mg m^{-3}, 0–300 m, and 0.01–1.14 m s^{-1}, respectively.

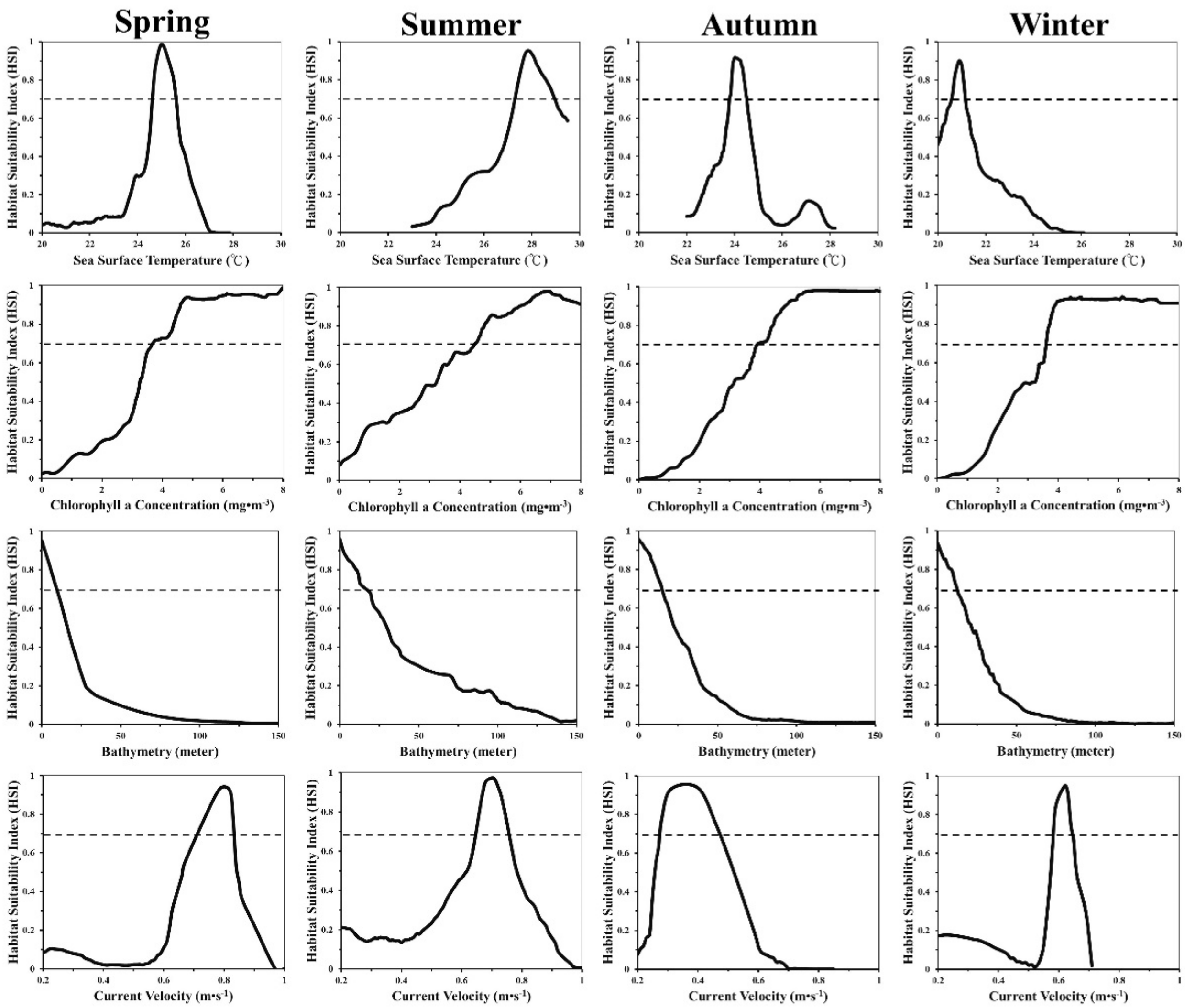

Figure 5. Response curves of environmental variables derived from the MaxEnt model by season. Horizontal lines indicate suitable environmental variable ranges for black sea bream in waters off western Taiwan.

3.3. Spatial Patterns of Habitat and Uncertainty

The black sea bream habitats were predicted, and the values were averaged seasonally together with the maps corresponding to uncertainty (i.e., SD) from spring to winter (Figure 6). The spatial patterns relating to habitat predictions differed between seasons, with the potential habitats of black sea bream exhibiting changes in terms of spatial extent and magnitude from spring to winter. Inside the study area, the stable and suitable habitat areas for black sea bream corresponded to the regions where intensive fishing activities occurred. Potential black sea bream habitats were identified between 22.7° N and 25.1° N in spring (Figure 6, top panel). Prediction uncertainty was represented by SD values, which indicated whether a predicted habitat was stable over all four seasons and, therefore, highlighted the transient nature of potential black sea bream habitats in spring.

The distribution of potential habitats was concentrated in coastal waters off central and western Taiwan in autumn (between 22.4° N and 24.2° N) and exhibited low corresponding SDs in summer (Figure 6, bottom panel). Potential black sea bream habitats shifted further northward and southward (between 22.1° N and 25.1° N) in autumn, with areas of high suitability extending from 22.4° N to 23.7° N. Lastly, potential habitats with high suitability exhibited a similar pattern in autumn and were identified between 22.4° N and 23.5° N in winter. Areas of high suitability were concentrated in patches in coastal waters from central to northwestern Taiwan (e.g., 23.2° N–24.1° N) and exhibited low corresponding SDs.

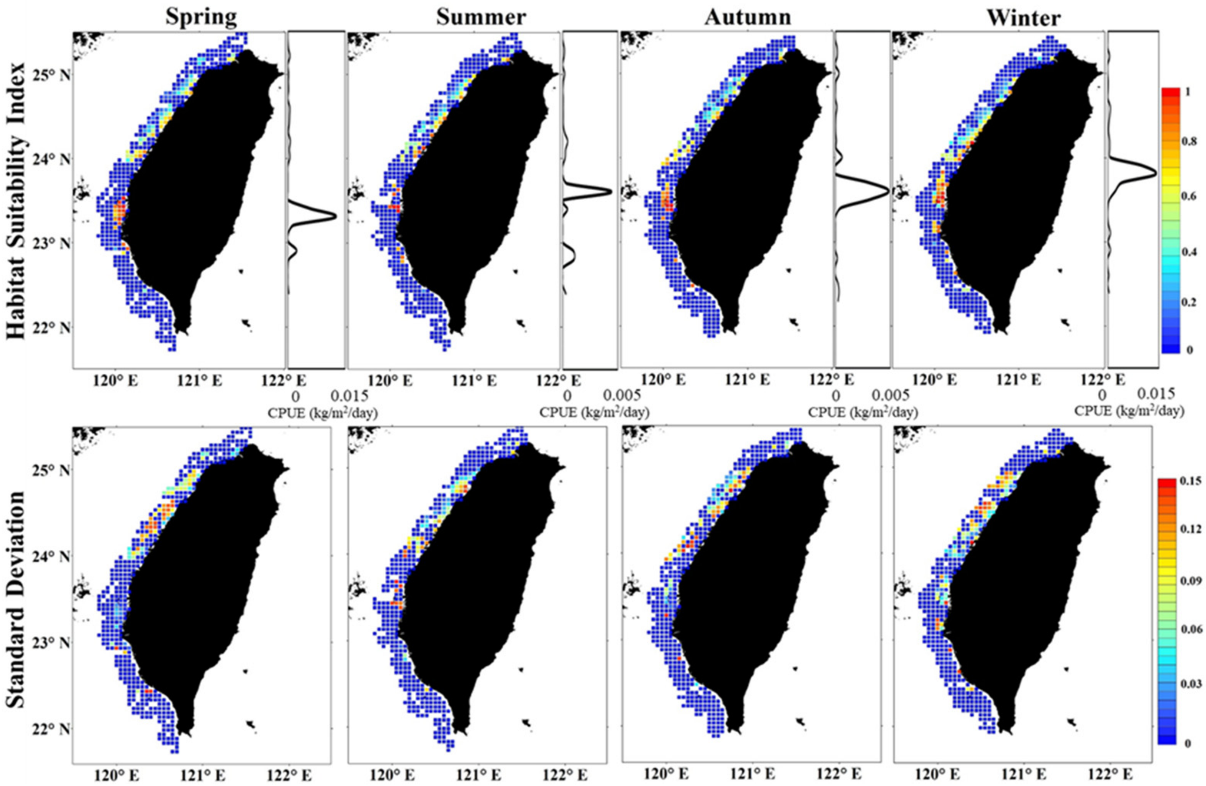

Figure 6. Habitat suitability index (top panels) and standard deviation (bottom panels) derived from the MaxEnt model by season. Top panels also indicate accumulated catch per unit effort by latitude.

The distribution of potential habitats in Chang-Yun Rise was similar in autumn and winter. However, the spatial patterns of associated uncertainty in Chang-Yun Rise were reflected in the high corresponding SDs that were observed. Overall, the suitable areas were concentrated in the 23.2° N–23.7° N range, and this was indicated by the low SDs throughout the year. This finding also indicated that the high accumulated CPUE of the vessels in our sample corresponded to latitude variation. The high CPUE that was identified at 23.3° N in spring shifted northward over time to 23.8° N in winter.

3.4. Validation of Habitat Model

The CPUE values were mapped seasonally and superimposed onto the HSI values estimated through the MaxEnt habitat model that utilized observed environmental data (Figures 3 and 6, top panel). Generally, the high CPUE values for each season were overlain on the HSI spatial maps, and higher CPUE values were observed in areas with higher HSI values for all seasons, excluding spring. The distribution of the low CPUE values (i.e., high effort) was observed in the coastal waters off northwestern Taiwan, which featured low HSI values. As expected, the spatial distributions exhibited seasonal variation.

The CPUE values for black sea bream were based on the HSI values predicted by the MaxEnt model for the entire year (Figure 7). The MaxEnt habitat model indicated that the increase in CPUE values corresponded to the increase in HSI values throughout the year, even though the CPUE values varied across seasons. In spring, the average CPUE was 0.0009 kg m^{-2}, when the HSI values ranged from 0.6 to 0.8, and the average CPUE was significantly higher (0.0011 kg m^{-2}) when HSI > 0.8. The average CPUE by HSI was lower in summer relative to the other seasons. The highest CPUE was 0.0008 kg m^{-2} for HSI values from 0.8 to 1.

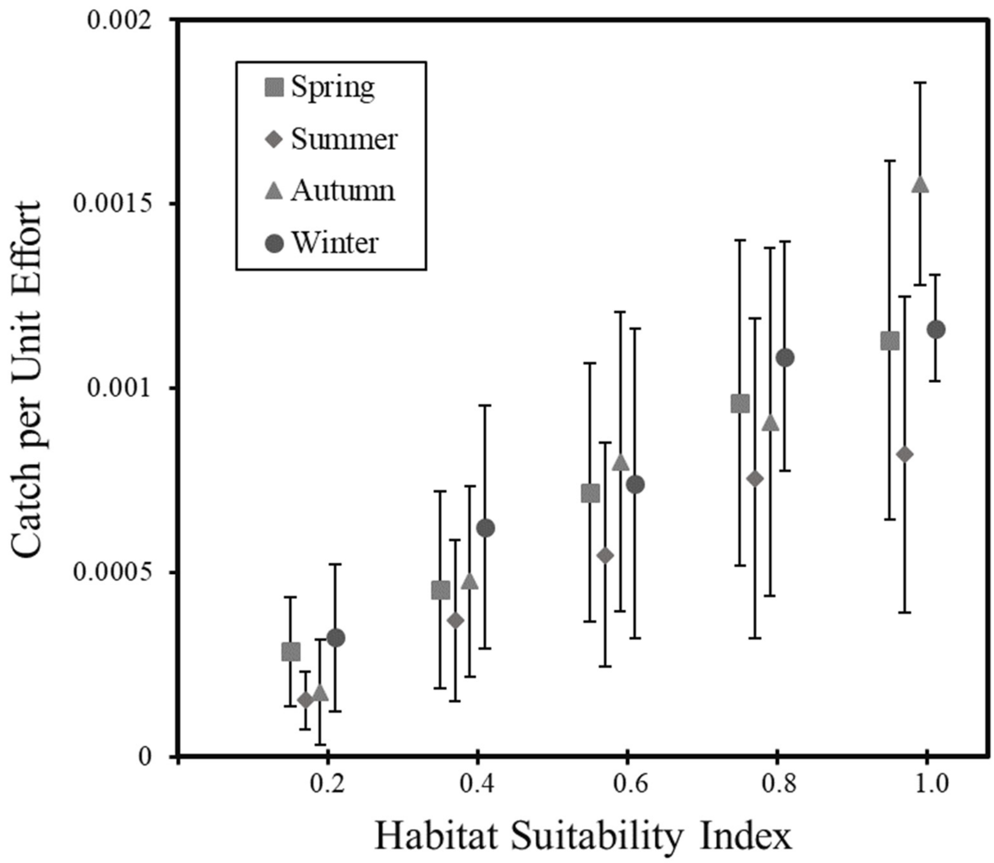

Figure 7. Relationships between the seasonal habitat suitability index (his) values estimated through the MaxEnt habitat model and average CPUE for the range of HSI (0.2 interval).

The average CPUE corresponded well for HSI values from 0.6 to 0.8 (0.0009 kg m^{-2}) and from 0.8 to 1 (0.0012 kg m^{-2}) for autumn. The average CPUE for HSI > 0.8 was significantly higher than for HSI values ranging from 0.6 to 0.8. The overall CPUE value was higher in winter than in other seasons. The average CPUE for HSI values > 0.8 was 0.0013 kg m^{-2}. Overall, winter (0.00041) and autumn (0.00046) had lower SDs and more stable values relative to the other seasons.

4. Discussion

4.1. Modeling the Habitat Distribution

Many fish species exhibit a characteristic spatial distribution pattern with habitat preferences related to their physiological needs or environmental tolerance [23]. In this study, we applied satellite-based remote sensing variables (i.e., SST, current velocity and Chl-a concentration) that have been commonly and routinely used in numerous studies to explore the spatial distribution of the species. Our research served as an opportunity to incorporate environmental data over wide ranges to develop species distribution models [31,57]. Few studies have examined occurrence data or current velocity, which were used in the present study to develop habitat models. The preliminary findings derived from the present study suggest that the examined species exhibits a unique spatial distribution pattern that corresponds to a combination of environmental variables.

The inclusion of fishery-independent data acquired through field surveys is still a challenge in modeling the habitat distribution of fish because the usefulness of data sourced from fisheries is affected by sampling quality, which should be evaluated before the collected data are used to conduct scientific research. An alternative method was applied in the present study; specifically, our fishery data were collected from a government management plan, and the data were reviewed by experts in this field to ensure the quality of the data that were same as obtained from the fishermen [24,58].

Species distribution models are widely employed to evaluate the habitat preferences of terrestrial and marine species [22]. However, the species-environment interactions associated with potential geographical distributions are complex and difficult to quantify. In the present study, the MaxEnt habitat model and a combination of available environmental variables hospitable to the black sea bream were used to identify the habitat hotspots and potential fishing grounds of the species in coastal waters off Taiwan. Moreover, the spatial and temporal patterns of habitat selection (i.e., seasonality pattern) were examined and determined based on the high suitability indices relating to the habitat. Seasonal periodicity has not been a major consideration in previous studies; however, the results of the present study indicated that it influenced black sea bream habitat distribution in space. The predictions and model uncertainty indicated seasonal variations in habitats, which, in turn, revealed the shift of the spatial distribution of the studied species.

4.2. Environmental Impacts on Habitat

The hydrological environment and current field in the TS are complex; this can be attributed to the presence of numerous canyons that cause complex current and hydrogeological changes when the KBC and SCSWC pass northwardly through the TS from the SCS to the ECS [59,60]. The KBC and SCSWC enhance the warming of SST in the TS in winter [61]. The strong flow of the KBC in coastal waters in summer and autumn may play a key role in influencing the habitats of several marine species [62]. In the present study, the spatial predictions of the MaxEnt models indicated that SST and current velocity led to significant seasonal variations in the habitat selection of black sea bream (Figure 4); this finding is highly correlated with the current system in the TS. Figure 2 indicates a higher production of black sea bream in the waters off southern and central Taiwan; however, the substantial seasonal movement of habitats indicated seasonal variation in production within the area (Figure 6).

A high concentration of *A. schlegelii* distribution was detected in waters with favorable SST, Chl-a concentration, bathymetry, and current velocity ranges (Table 2), which was in line with our expectations. This indicated that *A. schlegelii* selects preferred habitats that form potential fishing grounds with frequently high catches. The highest concentrations of black sea bream and their optimal habitats were observed within specific environmental ranges throughout the year (Figure 5). Our results are consistent with those of other studies [17]. The seasonal dynamics of *A. schlegelii* aggregation in spatial distribution were influenced by Chl-a concentration and water depth. The Chl-a concentration increased in autumn and winter in the waters off central Taiwan (Figure 4), and this trend corresponded to an increase of CPUE that resulted from an aggregation of fish in spawning grounds (Figure 6).

For the successful identification of species preferences and their optimal habitats, the selection of suitable environmental variables is crucial to the development of MaxEnt models or HSI modeling [63]. We discovered that the variables examined in the present model performed well when HSI modeling was incorporated into the MaxEnt habitat method. We could evaluate all possible candidate combinations according to a comparison of predictions and observations (Figure 7). However, the inclusion of other predictors in the habitat model may be helpful. For example, black sea bream may be influenced by the availability of prey, nutrient levels, thermal fronts, and dissolved oxygen concentration [64–66], all of which should be included in future analyses when the relevant data could be made available.

4.3. Spatial Aggregation and Seasonal Shift

Oyster farming in shallow waters was prevalent in the study area, particularly in the coastal waters off southern Taiwan [67]. Oysters and other larvae may serve as prey; hence, the study area could be a major feeding ground for black sea bream. The influence of oysters and larvae on black sea bream aggregation and spatial distribution was investigated in other studies. For example, Saito et al. [68] and Yamashita et al. [69] demonstrated that the annual production of oysters at Hiroshima Bay and Tokyo Bay was affected substantially by the presence of black sea bream in summer. Several environmental variables were used in the analyses conducted in other studies [68,69]; however, only a few variables were correlated to seasonal movement and spatial aggregation. To address this problem, a dimension reduction technique can be applied to potential variables (e.g., principal component analysis) to identify the interactions between complex environments and habitat distribution in space [70].

The positive relationship between HSI values and CPUE percentages is presented in Figure 7 to validate the modeling method. For all seasons, particularly for winter, HSI values higher than 0.6 were correlated with high CPUE for black sea bream. The spawning season of the studied species usually occurs from December to April [71,72]. Therefore, as was demonstrated in the present study, a higher CPUE is expected in winter because mature black sea breams may aggregate and become easy to be harvested during this period. Sadovy and Cornish [72] and Nakabo [73] also reported aggregations of black sea bream in coastal waters during the spawning season. Larvae and juvenile black sea bream tend to live in pelagic areas, whereas adult black sea bream live in benthic areas [41].

More than 80% of the fishing locations were in coastal waters, as reported by the sampling vessels in our database (Figure 8). This finding indicated that the fishermen followed the feeding grounds near the shore to catch black sea bream during the spawning season in the south section of the eastern TS. However, the fishing ground for black sea bream was located farther away from the shore because the central section of the TS (i.e., Chang-Yun Rise) is shallower than the north section of TS. The results from the MaxEnt habitat model indicated that the suitable habitats for black sea bream were located in the shallow coastal waters of the eastern TS, which featured a high Chl-a concentration, an optimal SST range of 20.6–28.9 °C, and a current velocity range of 0.28–0.83 m s^{-1}. When the identified associated uncertainty was taken into account, the habitat of black sea bream in the eastern TS mainly ranged from 23.3° N to 23.6° N and from 120.1° E to 120.3° E; this finding was determined using the MaxEnt habitat model and fishery and remote sensing data.

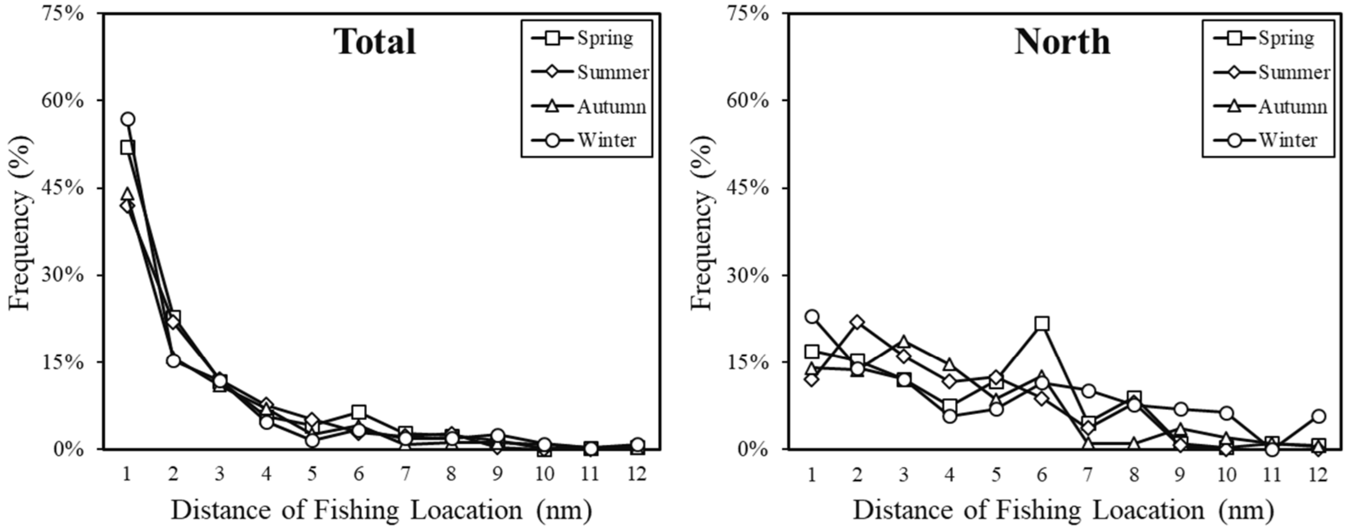

Figure 8. *Cont.*

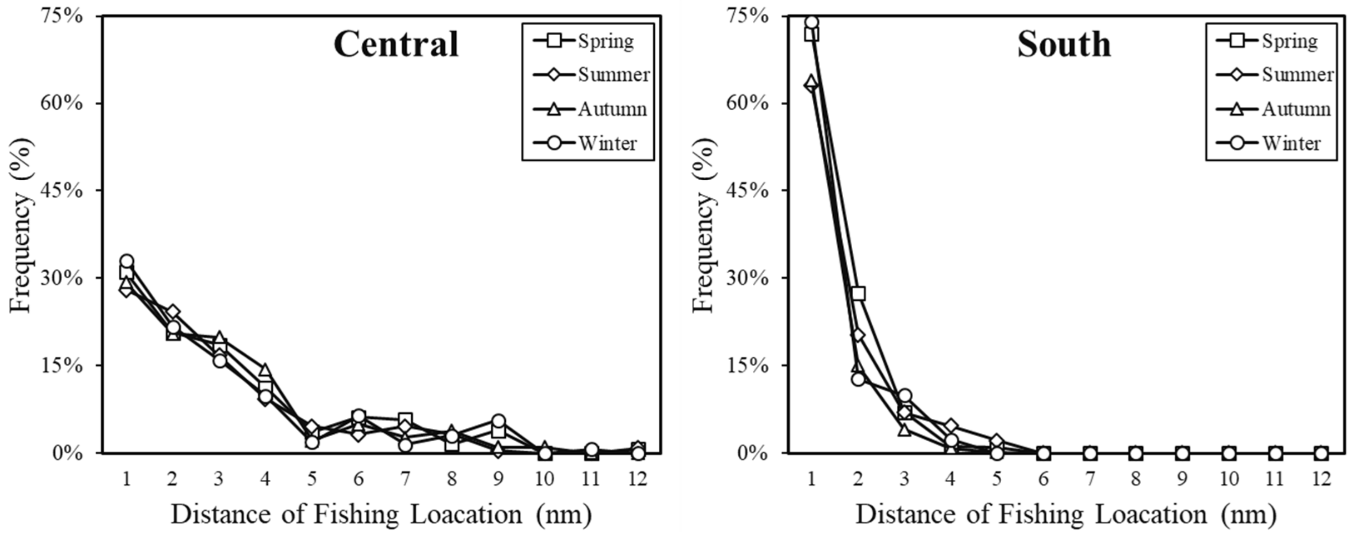

Figure 8. Distance of fishing location from the shoreline, as obtained by the sampling gillnet vessels for each season and area.

5. Conclusions

The seasonal variation in the habitat distribution of black sea bream was clarified using a new habitat modeling method (MaxEnt) that incorporated fishery and remote sensing data. High CPUE records were observed in coastal waters during the spawning season, and the species moved to the north of the TS. This finding was further verified by comparing the catch records and the spatial distribution of hydrological conditions in the waters off western Taiwan. We discovered that the seasonal selection of habitats with high HSI values was due to the biological needs such as the spawning and feeding behavior. The habitat models can be improved by increasing the resolution in both time and space. Among the environmental variables examined in this analysis, Chl-a concentration and bathymetry were revealed to be the most crucial variables in HSI modeling for black sea bream. Hotspot habitats (or the fishing ground) exhibited the following characteristics: high Chl-a concentration, shallow water (0–15 m), current velocity range of 0.28–0.83 m s^{-1}, and SST range of 20.6–28.9 °C. We found that the high HSI values (>0.7) used in the present study can identify suitable habitats for black sea bream, thereby providing essential information for scientific assessments based on habitat modeling.

Author Contributions: Conceptualization, S.-Y.T. and M.-A.L.; methodology, S.-Y.T., N.-J.S., M.-A.L. and R.I.S.; software, S.-Y.T.; validation, S.-Y.T. and N.-J.S.; formal analysis, S.-Y.T.; investigation, S.-Y.T., N.-J.S., M.-A.L., K.-W.L., J.-S.W., Y.C. and Y.-C.W.; resources, N.-J.S., M.-A.L., K.-W.L., J.-S.W., Y.C. and Y.-C.W.; data curation, N.-J.S., M.-A.L., K.-W.L., J.-S.W., Y.C. and Y.-C.W.; writing—original draft preparation, S.-Y.T.; writing—review and editing, M.-A.L., Y.-C.W. and A.H.V.; visualization, S.-Y.T.; supervision, N.-J.S., M.-A.L., K.-W.L., J.-S.W., Y.C. and Y.-C.W. All authors have read and agreed to the published version of the manuscript.

Funding: This study was partially sponsored through research grants from the Ministry of Science and Technology (MOST-100-2621-M-019-004) and the Fisheries Agency of the Council of Agriculture, Executive Yuan (104AS-17.2.1-FA-F1(Z), 105AS-14.2.1-FA-F1(Z), 106AS-13.2.1-FS-F1(Z) and 107AS-11.2.1-FA-F1(Z)).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data from this study are available from the corresponding author upon request.

Acknowledgments: We would like to thank two anonymous reviewers for their constructive comments and suggestions. Special thanks are given to the research team in the National Taiwan Ocean

University and the Fisheries Research Institute of the Council of Agriculture, Executive Yuan, for data collection and field survey under the support of research project: Investigation on the fishing activity and essential fish habitat for the databank of fingerling release species in coastal waters off Taiwan. This manuscript was edited by Wallace Academic Editing.

Conflicts of Interest: The authors declare no conflict of interest.

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